



Strong turbulence benefits toxic and colonial cyanobacteria in water: A potential way of climate change impact on the expansion of Harmful Algal Blooms

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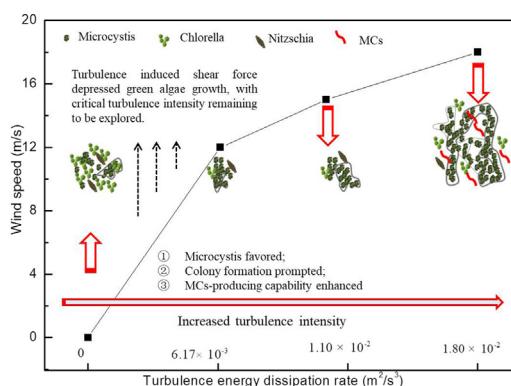
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HIGHLIGHTS

- Strong turbulence reduced algal density but the profile can be turned back.
- Turbulence triggered switches from *Chlorella* - to *Microcystis*-dominated state.
- Strong turbulence favored colonial *Microcystis*.
- The abundance of toxin-producing *Microcystis* was substantially induced.
- Phytoplankton can actively counteract the effects of strong turbulence.

GRAPHICAL ABSTRACT



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ABSTRACT

Extreme natural events such as typhoons can amplify the effect of hydrodynamics on the lake ecosystems. Here we presented data on the effect of typhoons on algal cell size based on field observation. Then turbulence simulation systems were used to decipher the response of natural phytoplankton communities to a range of turbulence regimes (linked to typhoon-induced turbulence intensity) under laboratory conditions. Turbulence intensities of 6.17×10^{-3} , 1.10×10^{-2} and $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$ benefited algal growth and triggered abrupt switches from unicellular *Chlorella* dominated to colonial *Microcystis* dominance, and the abundance of colonial algae depended on the turbulence intensity. Under the influence of elevated turbulence, *Microcystis* dominated biomass increased by 2.60–6.58 times compared with that of *Chlorella*. At a given phytoplankton density and community composition, we observed a significant increase in extracellular microcystins (MCs) and a 47.5-fold increase in intracellular MCs with intensified turbulent mixing, suggesting that the damage of algal cells concomitantly the stimulation of toxin-producing *Microcystis*. Our results confirmed that the formation of large colonial algal cells, enhancement of the succession of algal species, and most importantly, the induction of toxin-producing *Microcystis*, were the active adaption strategy when phytoplankton were impacted by strong

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turbulence. The result implies that the ongoing climate changes and typhoon events are likely to contribute to undesirable outcomes concerning phytoplankton populations.

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1. Introduction

Phytoplankton blooms impart negative effects on aquatic ecosystems and human beings (Amanda et al., 2011). Some bloom-forming phytoplankton is capable of producing a wide range of toxins such as microcystins (MCs), which can alter the antioxidant system and induce oxidative stress in aquatic species (Li et al., 2016). The growth and community structure of phytoplankton can be regulated by a variety of environmental conditions, for example, climate changes and hydrodynamic alternations (Choi et al., 2017; Rao et al., 2018).

Typhoons are extreme episodic, turbulence-inducing weather events and can affect aquatic ecosystems residing in low and middle latitudes (Tsuchiya et al., 2015). Studies have shown that typhoons can stimulate algal growth through vertical mixing by enhancing available nutrients (Ko et al., 2017). In the months following the passage of typhoons, chlorophyll A (Chl-a) masses have been found to be higher than storm-free periods (Ding et al., 2012; Zhu et al., 2014). Turbulence, a ubiquitous and inherent characteristic of aquatic ecosystems, serves as a major driver of change in physicochemical characteristics of the water column and can be substantially enhanced during typhoon events (Ding et al., 2016), which may impact the growth of phytoplankton.

Numerous studies concerning the effects of turbulence on the algal growth and physiological activities have been performed. Previously, turbulence was found to affect a wide range of biological processes, mostly related to the bulk distribution of algal cells in water (Francesc and Marrase, 2000). Recent studies confirm that turbulence can affect algal growth in multiple ways (Kang et al., 2019; Yu et al., 2018), for example, weak turbulence promotes the growth rate of the bloom-forming cyanobacterium *Microcystis* (Qin et al., 2018). The role of turbulence on phytoplankton is not only the direct, such as through cell division and pigment content (Thomas et al., 1995), but also indirect, including processes such as photosynthetic radiation (through increasing turbidity), thermal stratification (through enhancing mixing) and nutritional dynamics (sediment resuspension and nutrient regeneration) (Cabecinha et al., 2009; Naselli-Flores and Barone, 2000). Turbulence also promotes nutrient transport to algal cells, thus favors nutrient uptake, especially at low nutrient levels (Barton et al., 2015; Zhang et al., 2017). Mechanical damage such as broken cell walls and impaired organelle function can also occur under elevated turbulence mixing (Thomas and Gibson, 1990). Increasing turbulence intensity (illustrated by the turbulence energy dissipation rate, ϵ , m^2/s^3) causes a dramatic shift from the cyanobacterial to diatom and green algal dominance (Huisman et al., 2004), and weak wind-induced disturbances can increase the colonial size of the bloom-forming *Microcystis*, enabling it to overcome the effects of mixing (Qin et al., 2018). Changes in phytoplankton species may occur because the alternation of hydrodynamic conditions could cause the resuspension of sediment and release of internal nutrients, thereby affected the available light or nutrients (Zhang et al., 2015; Zhou et al., 2016), helping algae with higher growth rates and lower nutrients requirements to outcompete.

To date, the impact of small scale of hydrodynamic- or wind-induced turbulence on algal growth are frequently investigated since the studied turbulent dissipation rates are more likely to appear in lakes. Under extreme wind speeds, such as typhoon-induced strong turbulent mixing, field observations have confirmed the promotion of both phytoplankton biomass and algal cells size, whereas the concern about how to achieve the shift was not fully understood. In addition, despite substantial evidence demonstrating that turbulence can regulate algal growth, most studies have focused on a few species, especially the common bloom-former *Microcystis*. Few studies have assessed turbulence's impact on

natural phytoplankton communities. Additionally, current literature emphasizes passive phytoplankton responses to harsh environmental conditions such as turbulence, but it is highly possible that phytoplankton could actively counteract the effects of turbulence (Kang et al., 2019). Nevertheless, the ways in which strong turbulence restructures the natural phytoplankton community, and how the algal communities actively responded to the turbulent condition, have not been systematically investigated.

To address these knowledge gaps, approximately homogeneous turbulence simulation systems (AHTSs) were employed to generate turbulence. The turbulence intensities were regulated to simulate the typhoon-induced turbulence mixing levels. The phytoplankton density, potential maximum photosynthetic capacity, algal assemblage pattern and phytoplankton community composition were examined and evaluated. Extracellular polymeric substance (EPS), algal size and MCs were also analyzed. Based on the simulated microcosm study, we attempted to examine the effects of typhoon-induced turbulence on phytoplankton communities and to elucidate how the phytoplankton actively responded.

2. Materials and methods

2.1. Toxin standards and reagents

MCs standards (MC-RR, the most frequent MCs variants in Harmful Algal Blooms (HABs) waters (He et al., 2018)) were obtained from Taiwan Algal Science, Inc. (purity $\geq 95\%$ by HPLC). Methanol used for MC-RR analysis was of HPLC grade and other reagents used in our experiments were analytical reagent.

2.2. Microcosm incubation experiment

HABs water was collected from the surface water (0–0.5 m) of the Mingzhu Lake (with average depth of 2.0 m) on the campus of Chongqing University, during a cyanobacterial blooms in Aug, 2017. The laboratory study was performed in approximately homogeneous turbulence simulation systems (AHTSs), which were clearly described in our recent study (Kang et al., 2019). Briefly, the ϵ value was acquired through manipulating the grid oscillation distance and frequency (Fig. 1), and was estimated from previous literature (Michallet and Mory, 2004):

$$\epsilon = 0.45 f^3 S^2 / (S/M) \quad (1)$$

where f is the grid oscillation frequency; S is the vertical oscillation distance and M is the grid mesh size (distance between adjacent bars).

To make the turbulence intensity studied in the laboratory study comparable to the wind speed, the turbulence intensity was then determined from the previous literature that describing the turbulent dissipation rate as a function of wind speed in aquatic environments (Mackenzie and Leggett, 1993), then the turbulence intensity can be converted to wind speed.

$$\epsilon = 5.82 \times 10^{-6} \omega^3 / h \quad (2)$$

where ω is wind speed (m/s) and h is the water depth (m).

Each reactor of the AHTSs was filled with 7 L water that had previously been filtered through 80 μm mesh to allow phytoplankton to pass through but to exclude zooplankton (Symons et al., 2012). Twelve AHTSs, each containing the same volume of algal water, were divided into four groups, of which the ϵ values were adjusted to 0 (static water, controls), 6.17×10^{-3} , 1.10×10^{-2} and $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$, respectively,

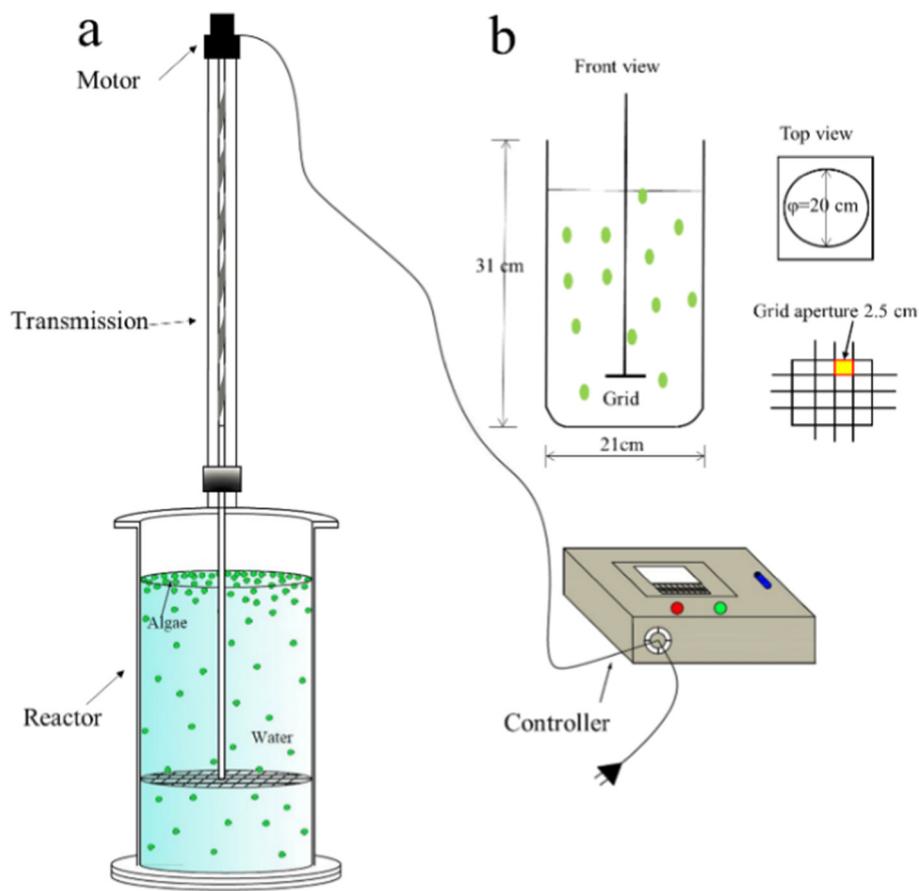


Fig. 1. Illustration of the simulated approximately homogeneous turbulence simulation systems (AHTSs) system in this study. a, illustrated the physical structure of AHTS and b showed the structure of the reactor.

with triplicates each. Theoretically, the studied ϵ values were equal to 0, 12.85, 15.58 and 18.36 m/s wind speeds when the depth of the lake was 2.0 m (Eq. (2)), and the wind speeds were close to the maximum reported wind speed in Lake Taihu (17.1 m/s (Li et al., 2018)). The average initial algal density in the four groups was 1.12×10^9 cells/L, 1.16×10^9 cells/L, 1.23×10^9 cells/L, 1.21×10^9 cells/L, respectively. The AHTSs were operated at 25 °C with an alternating cycle of 12 h of light and 12 h of darkness with a light intensity of 3300 lx.

2.3. Sample collection and preparation

Ten milliliters of water sample was collected from the middle of the reactor (approximately 10 cm below the water surface) every day during the microcosm incubation experiment. Phytoplankton were settled for identification and counting after being fixed by 1.5% Lugol solution. Then a 24-h sedimentation method was used to concentrate the phytoplankton sample to approximately 3 mL. A 0.1 mL subsample was taken and loaded into a 0.1 mL plankton counting chamber. Finally, the phytoplankton was counted everyday under an optical microscope (Leica DMLB, Germany) at 400 \times magnification. At the start and end of the study, phytoplankton composition analysis were performed based on the results of phytoplankton identification, of which the samples observed on the plate were identified to genus level using the identification key according to their morphological properties (Hu and Wei, 2006). The algal assemblage patterns (unicellular, colonial) were enumerated in random fields, and at least 200 individuals of the most frequent species were counted to distinguish, during which colonies were counted as cells, and the total number of algal cells in the colony was determined with the assistance of Algacount T300 System (Shinesco Technology Co., Ltd., Hangzhou, China). A pulse-amplitude-modulated

fluorometer AquaPen-C (AP-C100, Photon Systems Instruments, Czech Republic) equipped with a FluorPen 1.0 software was employed to measure the maximum quantum yield for the primary photochemistry (F_v/F_m) of samples that was dark-acclimated for 20 min prior to measurement. Hence the initial F_v/F_m of phytoplankton in each treatment was approximately 0.46. Algal cell sizes at the end of the study were also assessed using particle size distribution (PSD, Mastersizer 2000, England). The Excitation-Emission Matrix (EEM) fluorescence of EPS was measured using a Hitachi F-7000 fluorescence spectrometer (Hitachi High Technologies, Tokyo, Japan) at room temperature (25 ± 1 °C). The scanning ranges were 200–450 nm for excitation and emission. MC-RR, which was the most frequently detected MCs congeners (Li and Pan, 2015; Li et al., 2017), was determined at the end of the experiment. For extracellular MC-RR, 1 L water samples were applied to a preconditioned octadecylsilyl (ODS) cartridge after filtration through a Whatman GFF glass fiber filter, and then the toxins were eluted with 100% methanol and evaporated to dryness using a rotary evaporator (Büch, Germany), and the residue was redissolved with 1 mL of 90% methanol and stored at –20 °C until determination. With respect to intracellular MC-RR, the water samples were filtered through 0.22 μ m filters (mixed cellulose ester membrane) to obtain the algal cells, which were then freeze-dried and extracted using a 5% (v/v) acetic acid with ultrasonication (300 W, 5 min) for three times. After centrifugation at 8000 rpm for 10 mins, the supernatant was collected and followed by application to ODS cartridge, as was described above.

2.4. MCs determination

HPLC analysis was performed using a Shimadzu LC-10A system with two LC-10A pumps and a UV detector. The elution conditions were 60%

solution A (100% methanol) and 40% solution B (0.05 M KH_2PO_4 , pH = 3) at a flow rate of 1 ml/min well in using a Shimadzu Gasketing (CLO-ODS 6.0 × 150) column. The column temperature was maintained at 40 °C and the injection volume was 10 μL . The limit of quantitation is 0.02 g/L. The detailed information was available in our previous literature. Detailed information can be found in our previous study (He et al., 2018).

2.5. Statistical analysis

Statistically significant differences between the controls and treatments were compared using one-way and two-way analyses of variance (ANOVA). A comparison with a p -value ≤ 0.05 was considered significantly different.

3. Results

3.1. Impacts of typhoon events on phytoplankton from field observations

Typhoons events often cause devastating influences on human properties and trigger many environmental alterations in aquatic ecosystems. In the South China Sea, it was revealed that typhoon events triggered a 30-fold increase in surface Chl-a concentration (Lin et al., 2003). Additionally, typhoon events were capable of increasing the algal biomass and inducing the formation of large algal cells, in both fresh water (Qin et al., 2018) and oceans (Frenette et al., 1996). The reported results mostly focused on coastal regions where typhoon events seemed to occur more frequently than inland waters. Nevertheless, the available field observations suggest algal cells were larger in water systems found in typhoon-occurring regions or periods (Table 1), while the ways these variations are achieved remains to be explored. Accordingly, the microcosm experiment was conducted to study the ways in which the phytoplankton responded to strong turbulence mixing.

3.2. Microcosm experiment

3.2.1. Phytoplankton density

In the static systems (controls), the motile algal species gathered at the water's surface. Hence, constant decreases in algal density in the middle of the water column were observed (Fig. 2a). In contrast, turbulence triggered an increase in algal density. During the initial 6 days, the algal density consistently decreased with ϵ value of 6.17×10^{-3} , 1.10×10^{-2} and $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$; then showed an obvious increase afterwards. After 15 days incubation, the maximum algal density was maintained at 1.67×10^9 cells/L with ϵ of $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$ (Fig. 2a), which was significantly higher than its initial level. Fig. 2a also illustrated that turbulence favored algal growth compared to the controls, and as turbulence intensity increased, the algal growths were augmented ($p < 0.05$) (Fig. 2b).

3.2.2. Potential maximum photosynthetic capacity

In the control groups, despite Fv/Fm showing an abrupt increase before day 3, a constant decrease occurred afterwards; then, it was maintained at approximately 0.43 from day 15 on (Fig. 3a). In contrast, turbulence treatment was responsible for nearly a 1.5-fold increase of the Fv/Fm. The responses of Fv/Fm to varied ϵ were most obvious

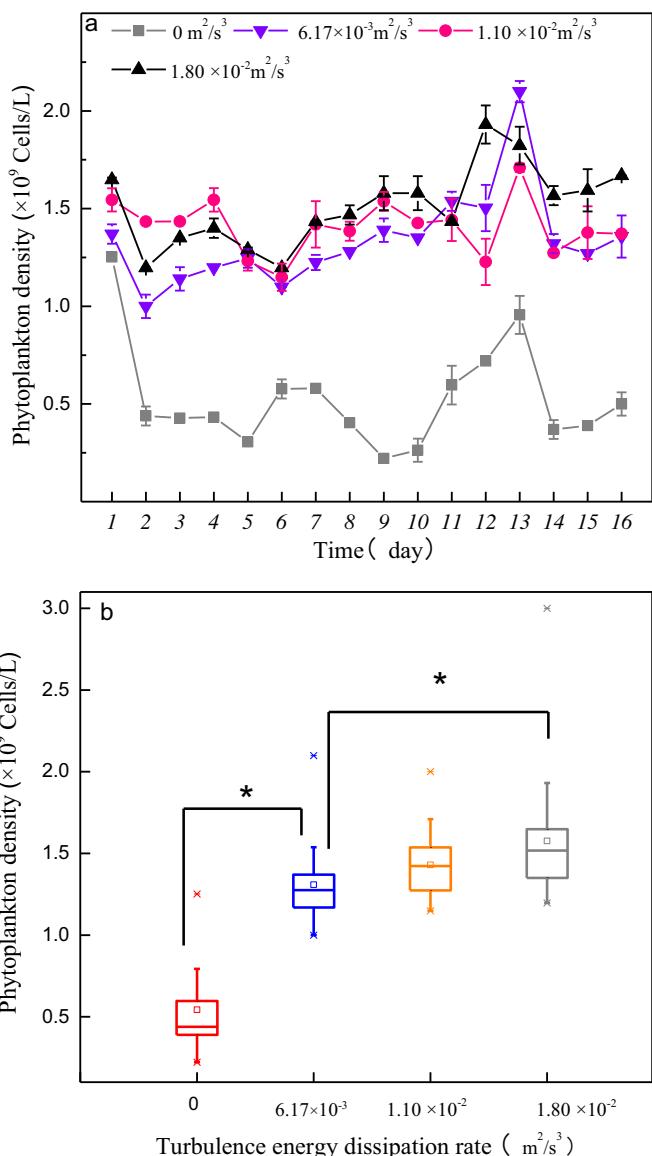


Fig. 2. Temporal variability of phytoplankton density (a) and its density ranges (b) over the span of 15 days of incubation.

from day 5 in the turbulent systems, but insignificant differences were shown when ϵ were ranged from 6.17×10^{-3} to $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$ (Fig. 3b, $P > 0.05$). Although ϵ value of $1.10 \times 10^{-2} \text{ m}^2/\text{s}^3$ caused the most severe depression of Fv/Fm before day 5, it was then largely promoted and exhibited the maximum value among the turbulent systems after 15 days of incubation (Fig. 3b).

3.2.3. Phytoplankton species and assemblage pattern

The phytoplankton population in water samples was primarily composed of 3 phyla: *Bacillariophyceae*, *Cyanobacteria*, and *Chlorophyceae*.

Table 1

Description of the response of phytoplankton community and algal cells size to typhoon events from the available literatures.

Site	Typhoon	Maximum speed (m/s)	Dominant phytoplankton		Algal size (μm)		Reference
			Before typhoon	After typhoon	Before typhoon	After typhoon	
Taihu	Morakot	11.8	<i>Microcystis</i>	<i>Microcystis</i>	20.2	70.1	(Qin et al., 2018)
Sagami Bay	Malou	25	<i>Protoperidinium</i>	<i>Chaetoceros; Cerataulina</i>	20	50	(Tsuchiya et al., 2017)
South China Sea	Kaemi	40	<i>Thalassiosira; Nitzschia</i>	/	>20 (50%)	>20 (60%)	(Li et al., 2009)
Lake Biwa	/	20	Typhoon-induced mixing stimulated the shift to fast-growing larger cells				(Frenette et al., 1996)

/: indicating data not recorded.

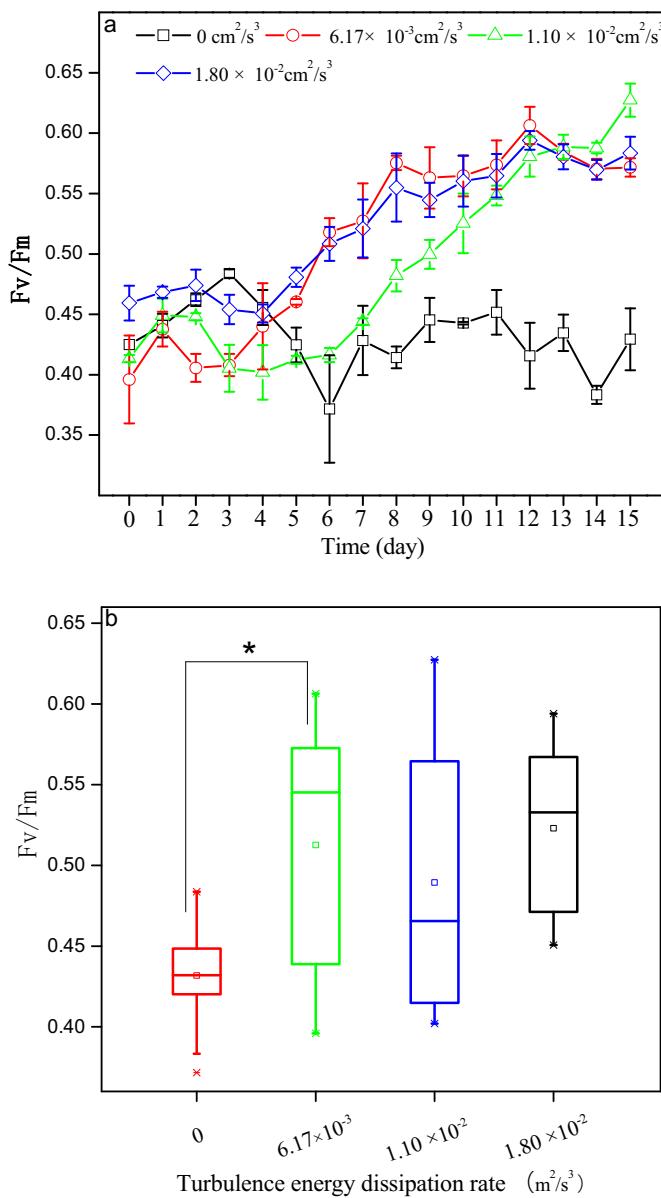


Fig. 3. Dynamics of F_v/F_m (a) and its value ranges (b) over the span of 15 day of incubation.

Nitzschia sp., *Microcystis* sp., and *Chlorella* sp. were the most representative algal species and accounted for 5.90%, 75.50% and 18.20% in the raw water, respectively (Fig. 4a). Cyanobacteria were the dominant phylum in the experimental systems. However, the abundance of *Chlorella* sp. abruptly increased to 72.7%, and ultimately becoming the dominant species in the controls after 15 days. On the other hand, *Microcystis* sp. played a key role in the composition of the community, which were approximately 2.99, 2.60 and 6.58 times as high as that of *Chlorella* with ϵ of 6.17×10^{-3} , 1.10×10^{-2} and $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$, respectively. The amount of *Microcystis* increased with enhanced turbulence intensity and became the dominant species in the plankton community, and its abundance was accompanied by the intensified turbulence intensity (Fig. 4a).

The composition and structure of phytoplankton communities were further illustrated as algal assemblage patterns (unicellular and colonial) (Fig. 4b). In the raw water, colonial algae (mainly *Microcystis*) were significantly higher than the unicellular pattern (mainly *Chlorella*). However, unicellular algae were more prevalent in the static systems after 15 days of incubation, accounting for >86.2% of the total phytoplankton biomass (Fig. 4b). Colonial phytoplankton dominated the

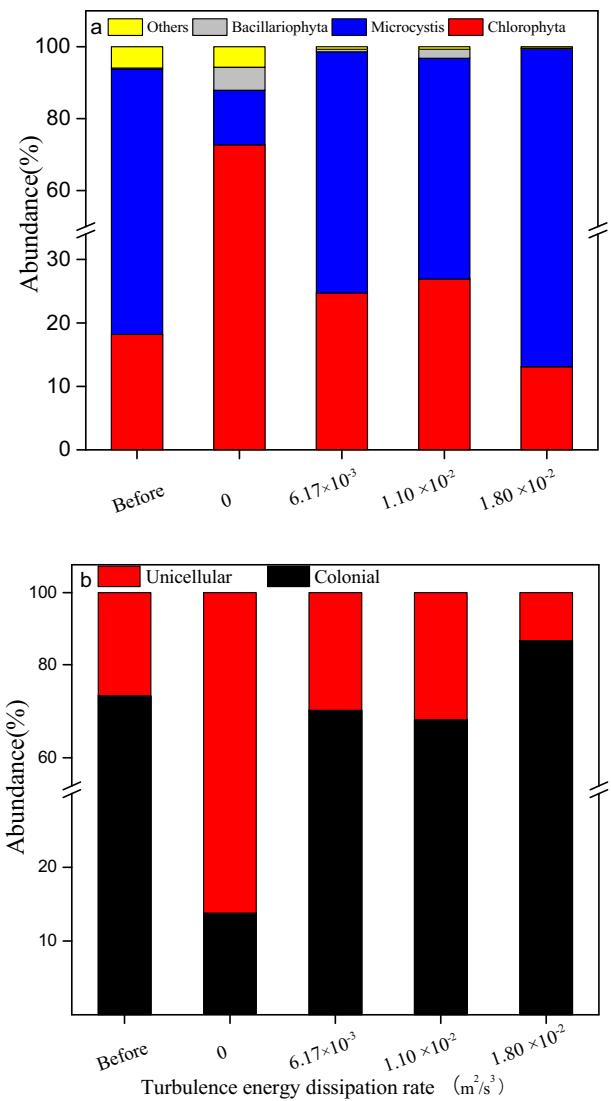


Fig. 4. Phytoplankton community composition (a) and algal assemblage patterns (b) for each treatment at the start and the completion of the incubation.

assemblage patterns in turbulent water (Fig. 4b), mainly composed of *Microcystis* sp. (Fig. 4a). The abundance of colonial algae was positively related to the turbulence intensity (from a turbulence intensity of 6.17×10^{-3} to $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$, the colonial algae accounted for 69.50% to 86.2%, respectively).

3.2.4. Algal cells size

The results of PSD analysis revealed that the mean particle diameters of algal cells in the raw water were $91.26 \mu\text{m}$ with a median diameter $d_{(0.5)}$ of $74.27 \mu\text{m}$. Under turbulent conditions, the mean particle diameters increased to 108.2 , 121.8 and $143.6 \mu\text{m}$ after 15 days incubations, which were 1.18-fold, 1.33-fold and 1.57-fold higher than before, respectively. In contrast, the mean particle diameter remained at $45.24 \mu\text{m}$ in the controls (Fig. 5). These data confirmed that strong turbulence favored colonial algae.

3.2.5. Variations in fluorescence EEM

Fluorescence EEM is a rapid, selective, and sensitive technique for distinguishing groups of organic compounds in water. According to previous reports, the peak observed at E_x/E_m 275/320–335 nm correlated to protein-like substances containing tryptophan (Ni et al., 2017) (peak A in the present study). Peak B (230–235/305–330 nm) could be identified as aromatic proteins including tyrosine (Ni et al., 2017).

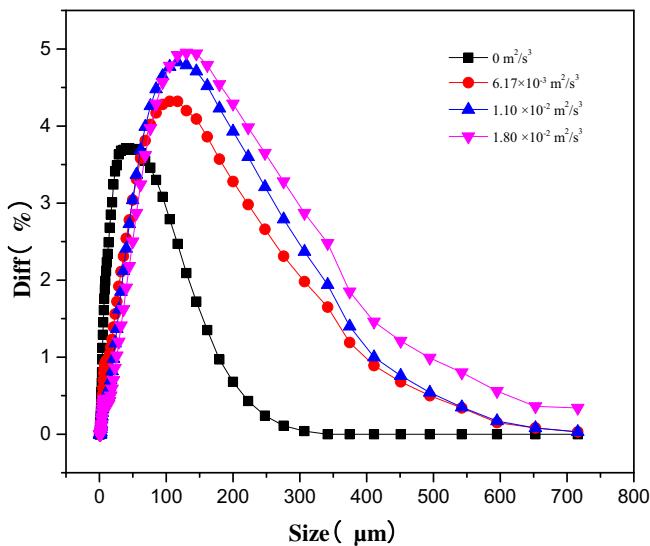


Fig. 5. The particle size distribution of algal cells in the control and turbulent systems.

The release of extracellular proteins substantially increased with increasing turbulence intensity (Fig. 6), indicating that algal cells lysed and then released intracellular proteins, which may have been helpful for the formation of colonial algal cells. This finding is consistent with the analysis of algal assemblage patterns (Fig. 4b), which showed the colonies could be largely induced with increased turbulence mixing.

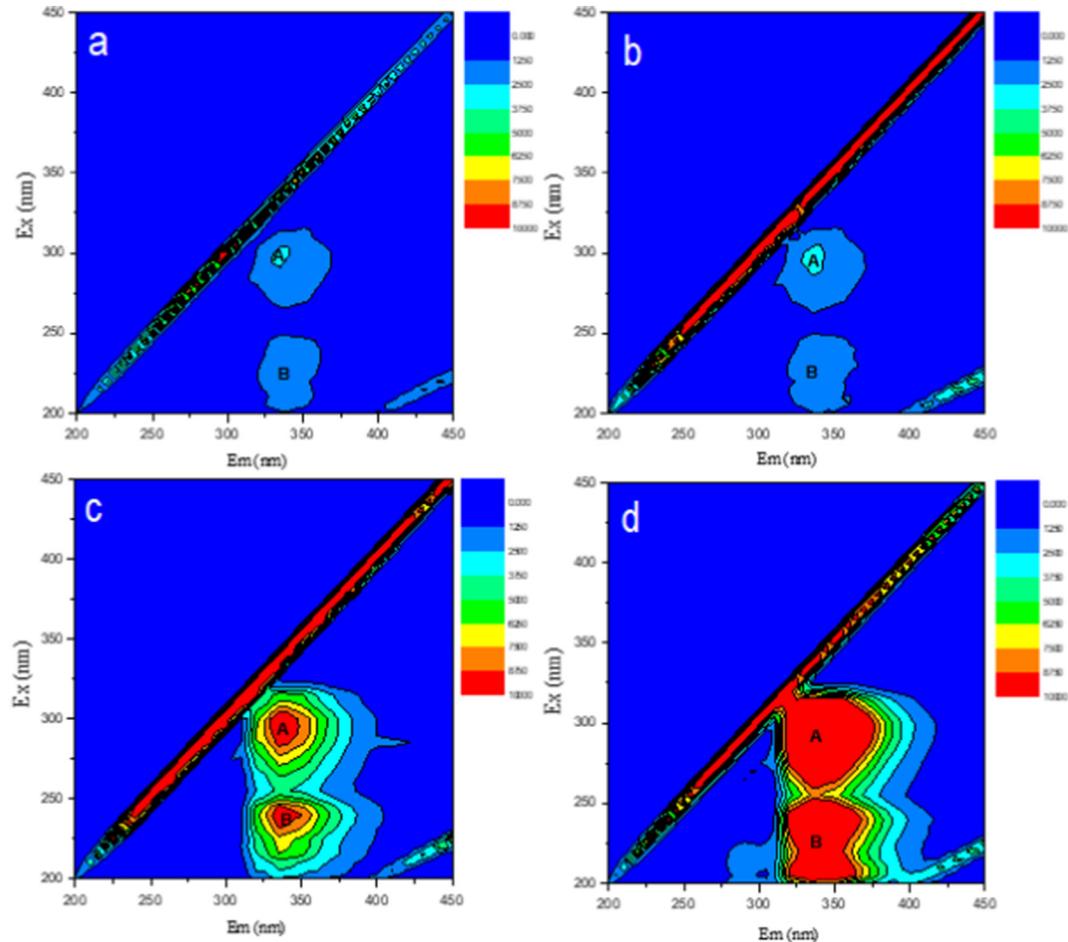


Fig. 6. Fluorescence excitation-emission matrices for EPS in the four systems after 15 day of incubation. a, b, c and d indicate ε value of $0, 6.17 \times 10^{-3}, 1.10 \times 10^{-2}$ and $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$, respectively.

3.2.6. MC-RR content

After 15 days' incubation, the intracellular MC-RR remained at 1891 $\mu\text{g}/\text{kg}$ in the controls, which were significantly lower than under turbulent conditions ($p < 0.05$) (Fig. 7a). With the intensification of turbulence mixing, algal cell damage was enhanced and the intracellular MC-RR should dramatically reduce compared to the controls. In contrast, in the turbulent systems, intracellular MC-RR significantly exceeded that in the controls and maximally reached 91,842 $\mu\text{g}/\text{kg}$ (ε value at $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$). On the other hand, the increasing turbulence intensity promoted algal lysis (Fig. 5b-d) and caused the release of intracellular MC-RR (Fig. 7b). As a result, extracellular MC-RR levels increased significantly in turbulent treatments and reached 1.21, 1.06 and 0.85 $\mu\text{g}/\text{L}$ for turbulence intensities of 6.17×10^{-3} , 1.10×10^{-2} and $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$, respectively, after 15 days.

4. Discussion

4.1. Strong turbulence promoted the algal biomass

Phytoplankton growth is crucial in supporting the food web and regulating material and energy flow in waters. Typhoons often induce large changes in natural habitats that may favor or depress phytoplankton growth. The responses of phytoplankton to typhoon-induced perturbations in coastal and adjacent marine waters were extensively studied (Pan et al., 2017; Tsuchiya et al., 2015; Zhou et al., 2011), and it was revealed that turbulence and nutrient concentration are dominant forces controlling the growth and physiological activities of phytoplankton (He et al., 2017; Heisler et al., 2008). In nutrient-rich and

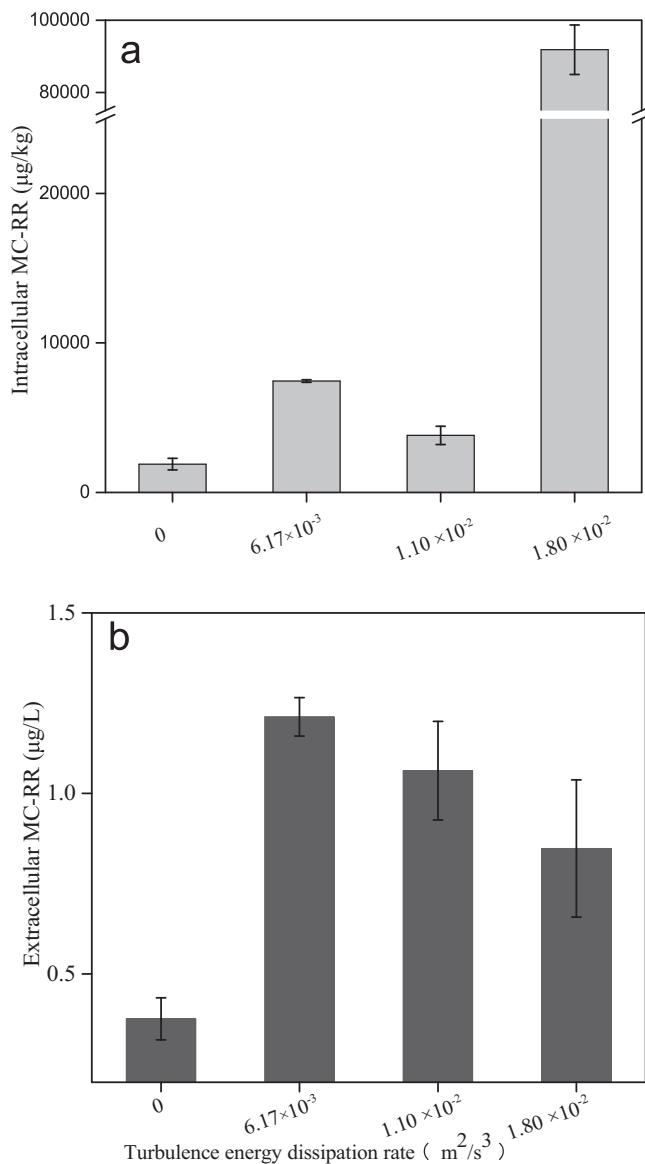


Fig. 7. Concentration of intra- (a) and extracellular (b) MC-RR at the completion of the incubation between treatments.

temperature-favorable fresh waters, variations in physical characteristics of water (e.g., the turbulence) are often accompanied by shifts in dominant phytoplankton.

In this study, several turbulence intensity levels were used to investigate the potential relationship between phytoplankton density and turbulence intensity, with the purpose of elucidating how the phytoplankton community responded to the strong turbulent conditions. A recent study showed that the effects of turbulence on algae physiology was evident by a 22% increase in the growth rate at ε of $8.5 \times 10^{-5} m^2/s^3$; however, the growth rate was suppressed when the ε value increased to $10^{-4} m^2/s^3$ (of which the ε value approaching 2 orders of magnitude lower than in our study) (Missaghi et al., 2016). In contrast with the previous literature, despite the algal density in the water column showing a dramatic decrease in the controls, the density increased in comparison to its initial value in the strong turbulent systems (with ε value in the range of 6.17×10^{-3} and $1.80 \times 10^{-2} m^2/s^3$) (Fig. 2), indicating the incubated phytoplankton community survived under the extremely high turbulence conditions. This finding was confirmed by our results that the F_v/F_m value, which was considered to be a sensitive photosynthetic parameter to any conditions that disturbing intracellular electron transport (Leupold et al., 2013),

increased during the study period (Fig. 3a) and was positively related to turbulence intensity (Fig. 3b), indicating that the photosynthetic capability of algae showed a slight disruption in response to the strong turbulence. This observation also agreed well with a recent study showing turbulence had a positive effect on the structure of PSII and F_v/F_m (Wang et al., 2012). The dynamics of algal density and F_v/F_m jointly indicated that although the algal density seemed to slightly increased during the study, the algal photosynthetic activities were largely altered, which may be due to the alternation of algal species, as algal competition may alter the outcome of phytoplankton communities. This finding was in accordance with the fact that the increasing turbulence intensity accounted for algal species changes (Fig. 4a).

4.2. Strong turbulence favored the growth of colonial *Microcystis*

The current study showed the increasing turbulence intensity largely promoted the abundance of *Microcystis* and its density significantly exceeded the value in the controls after 15 days of incubation (Fig. 4a), indicating strong turbulence helped *Microcystis* outcompete other phytoplankton species. These results are inconsistent with studies from numerical simulations showing that faster-growing *Chlorella* dominated in the turbulent water because *Microcystis* colonies and nonbuoyant phytoplankton were exposed to identical light conditions (Yu et al., 2018). Previous studies suggested that turbulence may impact phytoplankton growth and community structure by enhancing the nutrients flux into algal cells, thereby increasing the nutrients available for phytoplankton (Barton et al., 2015) or making it easier for algal cells to find the suitable light intensities and living spaces (Fraisse et al., 2015). In this study, the initial nutrient condition was similar among treatments, and under the equal phytoplankton densities and similar community compositions, the light intensity may also showed an indistinct difference among the turbulence treatments. Hence, under the well-mixed conditions in this study, chlorophytes, diatoms and cyanobacteria were exposed to similar light and nutrient conditions. Theoretically, the higher growth rates of green algae gave them a competitive advantage compared to *Microcystis* thus would favor their populations to recover from and overcome the dominance of *Microcystis* (Huisman et al., 1999), but the strategies of both buoyant *Microcystis* and fast-growing green algae may be disrupted in the strong turbulent water. A possible reason was that the shear force triggered by the strong turbulence damaged the algal cells of green algae, while the formation of colonial *Microcystis* may impair the loss of cell integrity via the secretion of adhesive EPS (Figs. 5 and 6). Accordingly, the green algae can be replaced by the cyanobacteria. Our hypothesis can be partly demonstrated by a recent study, in which the field observations (during the typhoon period and at a maximum speed of 13.8 m/s were recorded, close to the 12.85 m/s in our study) and laboratory controlled experiments found that disturbance mixing would prompt the large colony formation and increase the colonial buoyancy of cyanobacteria (Qin et al., 2018). However, monoculture and competition experiments should be combined to test the hypothesis, which calls for further studies.

4.3. High turbulence intensity favored toxin-producing *Microcystis*

The effect of weak turbulence on the growth of phytoplankton has received increasing attention in recent years, whereas its impacted on toxin-producing algal cells has not been studied. The results here showed strong turbulence prompted the abundance of *Microcystis* during which the formation of colonies may help impair the shear force to algal cells, and the predominance of MCs-producing *Microcystis* may further contribute to explaining the results. MCs occurrence is considered to be affected by a number of abiotic and biological factors (Neilan et al., 2013). Release of MCs into water can occur during cell death but can also be due to environmentally mediated circumstances such as allelopathy between algal species (Merel et al., 2013). Previous studies have shown that there are two ways of contributing to the

concentrations of dissolved MCs: increasing the abundance of MCs-producing cyanobacterium and inducing the MCs production capability of toxicogenic strains (Wiedner et al., 2003). Intracellular MCs can be released into the surrounding water once the algal cells undergo stress or cell damage occurs (Li et al., 2016), hence the increase of extracellular MCs is often accompanied by the reduction of intracellular MCs. However, in the present study, both the intra- and extracellular MC-RR showed significant increase with the intensified turbulence mixing (Fig. 7). These results agreed well with a previous study that suggesting the increase of MCs concentration is a direct function of toxin cell proliferation as promoted by turbulence (Neilan et al., 2013), indicating the abundance of toxin-producing *Microcystis* was largely prompted in turbulent water, which may help *Microcystis* outcompete green algae. This effect can be supported by the outcome of the phytoplankton community succession (Fig. 4a).

4.4. Phytoplankton actively counteracts the effects of strong turbulence

Turbulence can manipulate phytoplankton growth or community composition in many ways including nutrient assimilation (Chengala et al., 2013), photosynthesis (Wilkinson et al., 2016), algal movement (Ebert et al., 2001; Huisman et al., 2002), and light accessibility (Yu et al., 2015). The above mentioned literature highlighted how turbulence influenced algal cells or phytoplankton, these studies mainly revealed the passive response of phytoplankton (Table 2) while their active strategies in combatting the stress are largely unexplored.

In this study, we paid special attention to the ways in which the phytoplankton adapted to turbulence. Based on the acquired data, we proposed several strategies possibly explaining the results when the phytoplankton community was under the impact of strong turbulence. First, toxic *Microcystis* outcompetes other phytoplankton, but causes the reduction of algal diversity. As illustrated in Fig. 4a, the abundance of *Microcystis* sp., increased from 73.9% to 86.2% when the turbulence intensities were in the range of 6.17×10^{-3} to $1.80 \times 10^{-2} \text{ m}^2/\text{s}^3$. Our results are supported by a recent study which documented the response of two algal species (diatom and cyanobacteria) under turbulence and showed turbulence is more beneficial for the growth of cyanobacteria (Zhou et al., 2016). The results also fitted well with the intermediate disturbance hypothesis, which suggested that excessive disturbance is intolerable for some species and so will reduce diversity (Grime, 1973). Second, the alternation of algae assemblage patterns is helpful in reshaping phytoplankton communities. Formation of large colonies plays an important role in freshwaters algal blooms. The size and morphology properties of algal cells, particularly colonial formation, could critically affect grazing pressure by zooplankton, migration velocities, and nutrient uptake (Li et al., 2018; Zhu et al., 2016). In our study, the abundance of colonial algae (mainly *Microcystis* sp.) in turbulent

treatments were significantly higher than that in the controls (13.8%) (Fig. 4b). The buoyancy regulation supported by gas vesicles helps *Microcystis* gain the competitive advantage in lakes, which are usually calm. However, *Microcystis* usually loses its advantage in relatively turbulent conditions. Therefore, a recent study suggested buoyancy regulation did not help *Microcystis* gain an advantage in turbulent water (Yu et al., 2018). Different from the literature, in our study, the *Microcystis* seemed prevalent in the tested turbulence intensity ranges, indicating alternative strategies (probably colonial formation) rather than gas vesicles may play an essential role. Moreover, the formation of colony cells was supported both by the abrupt increase in algal sizes (Fig. 5) and the fluorescence EEM analysis (Fig. 6), which clearly illustrated the release of protein-like EPS by the algal cells in turbulent water. EPS can affect the surface properties of algal cells through electrostatic binding, polymer bridging and a sweep strategy, thus exhibiting a strong impact on algal aggregation (Xu et al., 2014). Colony formation provides *Microcystis* with many ecological advantages, including the ability to adapt to varying light and poor nutrition (Xiao et al., 2018), and large colony sizes affords *Microcystis* the fastest floating velocity of freshwater cyanobacteria. They thereby outcompete other algae, as the latter are unable to grow adequately to sustain their populations. Overall, our study found that through the combined efforts of colonial algae formation, community dominance the community by *Microcystis*, and toxin-producing *Microcystis* induction, the phytoplankton adapted to the high turbulent environment (Table 2). These findings confirmed phytoplankton evolved diverse adaptive strategies, particularly the morphological and functional differentiation, to cope with the environmental stressors caused by the strong turbulence (Fig. 8).

4.5. Environmental implications

Long-term observations have documented that an extreme typhoon switches the primary producing community of lake ecosystems from macrophyte dominance to phytoplankton dominance (Ding et al., 2016), during which process the algal biomass and size can be substantially increased. Our results described the active adaption strategies of phytoplankton under the influence of strong turbulence. Some studies showed then increased frequency of typhoon events in the past 30 years was related to a concomitant increase in surface temperature that caused by global warming (Chan, 2008; Emanuel, 2005). As it was suggested that global temperature was projected to increase by 0.3–4.8 °C at the end of this century (Gong et al., 2019), the occurrence of typhoons would be potentially accelerated in the future. Previous studies had proven that typhoon events were responsible for the elevated algal biomass and increased algal size (Ding et al., 2012; Li et al., 2009). Our results revealed that the toxin-producing *Microcystis* (which may release more MCs in the surrounding water (He et al., 2018)) can be substantially induced in strong turbulent waters, to the best of our knowledge, for the first time. These findings indicated the ecological impacts of typhoon on lake ecosystems would be more severe than the observed results. In addition, despite our study emphasizing the alternation of algal community composition and assemblage patterns in response to turbulence mixing, it should be note that typhoon events also create a pulse of nutrient into the water column and cause the resuspension of sediment, which may also regulate the growth of phytoplankton, elucidating the joint impacts of hydrodynamic condition, nutrients availability and light penetration in typhoon events, calling for multi-disciplinary studies.

5. Conclusion

Typhoon events contribute to the occurrence of phytoplankton with larger algal sizes. Using turbulence simulation systems, our data explains how the outcome is achieved; hence, it provides empirical support for the responses of phytoplankton to increased turbulence. Strong turbulence (equal to wind speeds of 12.85 to 18.36 m/s) not

Table 2

Description of the relevant study concerning the impact of turbulence on phytoplankton communities.

Response of phytoplankton to turbulence	Reference
Passively (what the treatment influenced)	
Nutrient availability	Barton et al., 2015; Karp-Boss, 1996
Light attenuation	Yu et al., 2015; Yu et al., 2018
Living space	Fraisse et al., 2015
Shear force	Xiao et al., 2018
Cells metabolic process	Thomas et al., 1995
Actively (how the algae responded)	
Previously reported	
Cell size changes	Karp-Boss, 1996
Biological relationship	Francesc and Marrase, 2000
Buoyancy regulation	Huisman et al., 2004
Finding from this study	
Colonial algae formation	This study
Dominance the community by <i>Microcystis</i>	
Induction of toxin-producing <i>Microcystis</i>	

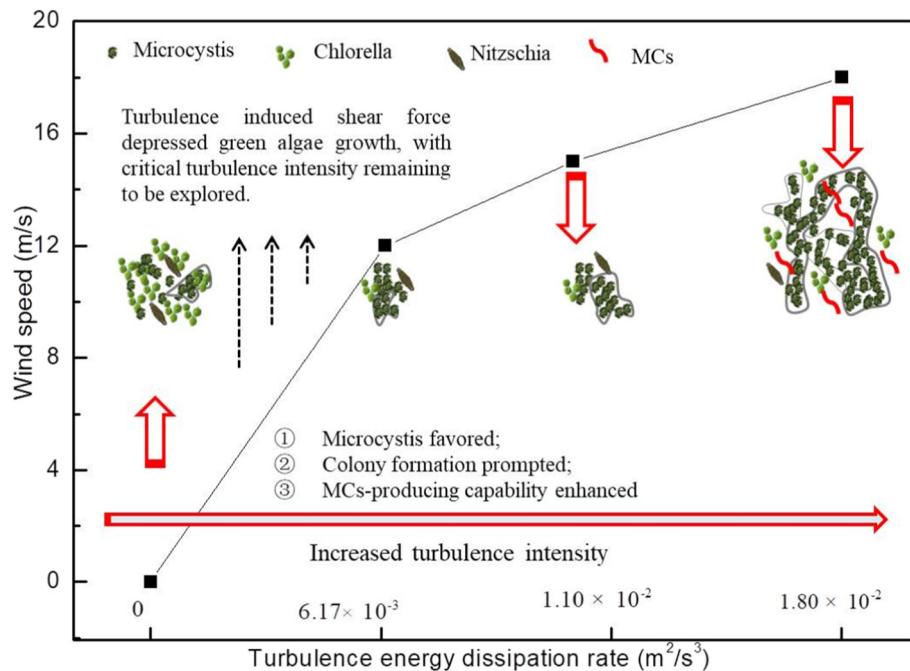


Fig. 8. Conceptual model of the response of phytoplankton to strong turbulence.

only triggered an increase in phytoplankton density after 15 days of incubation, but also resulted in larger size algae, which can be attributed to the following factors: 1) Turbulence favored the growth of *Microcystis* sp. instead of *Chlorophyta* sp. 2) The succession of algal species was accompanied by the alternation of an algal assemblage pattern from a unicellular algae to a colonial one, during which the release of protein-like EPS played an essential role. 3) The colonial *Microcystis* sp. dominating the phytoplankton communities were more prone to be toxin-producing strains. These results may contribute to a further understanding of the how strong hydrodynamic alternations such as typhoon-induced turbulence shapes phytoplankton community composition in lakes, thereby extending our current knowledge concerning the active survival strategies of phytoplankton in dynamic environments.

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Conflict of interest

The authors declare that they have no conflict of interest.

References

Amanda, E., Poste, R.E.H., Stephanie, J.G., 2011. Evaluating microcystin exposure risk through fish consumption. *Environ. Sci. Technol.* 45 (13), 5806–5811.

Barton, A.D., Ward, B.A., Williams, R.G., Follows, M.J., 2015. The impact of fine-scale turbulence on phytoplankton community structure. *Limnol. Oceanogr.* 4 (1), 34–49.

Cabecinha, E., Brink, P.J.V.D., Cabral, J.A., Cortes, R., Lourenço, M., Pardal, M.Á., 2009. Ecological relationships between phytoplankton communities and different spatial scales in European reservoirs: implications at catchment level monitoring programmes. *Hydrobiologia* 628 (1), 27–45.

Chan, J.C.L., 2008. Decadal variations of intense typhoon occurrence in the western North Pacific. *P. Roy. Soc. A* 464 (2089), 249–272.

Chengala, A., Hondzo, M., Mashek, D.G., 2013. Fluid motion mediates biochemical composition and physiological aspects in the green alga *Dunaliella primolepta* Butcher. *Limnol. Oceanogr.* 3 (1), 74–88.

Choi, B.J., Lee, J.A., Choi, J.S., Park, J.G., Lee, S.H., Yih, W., 2017. Influence of the tidal front on three-dimensional distribution of spring phytoplankton community in the eastern Yellow Sea. *Chemosphere* 173, 299–306.

Ding, Y., Qin, B., Zhu, G., Wu, T., Wang, Y., Luo, L., 2012. Effects of typhoon Morakot on a large shallow lake ecosystem, Lake Taihu, China. *Ecohydrology* 5 (6), 798–807.

Ding, Y., Qin, B., Xu, H., Wang, X., 2016. Effects of sediment and turbulence on alkaline phosphatase activity and photosynthetic activity of phytoplankton in the shallow hyper-eutrophic Lake Taihu, China. *Environ. Sci. Pollut. R.* 23 (16), 16183–16193.

Ebert, U., Arrayas, M., Temme, N., Sommeijer, B., Huisman, J., 2001. Critical conditions for phytoplankton blooms. *B. Math. Biol.* 63 (6), 1095–1124.

Emanuel, K., 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436, 686.

Fraisse, S., Bormans, M., Lagadeuc, Y., 2015. Turbulence effects on phytoplankton morphofunctional traits selection. *Limnol. Oceanogr.* 60 (3), 872–884.

Francesc, P., Marrase, C., 2000. Effects of turbulence on plankton: an overview of experimental evidence and some theoretical considerations. *Mar. Ecol. Prog. Ser.* 205, 291–306.

Frenette, J.J., Vincent, W.F., Legendre, L., Nagata, T., 1996. Size-dependent phytoplankton responses to atmospheric forcing in Lake Biwa. *J. Plankton Res.* 18 (3), 371–391.

Gong, Y., Wu, J., Vogt, J., Le, T.B., 2019. Warming reduces the increase in N2O emission under nitrogen fertilization in a boreal peatland. *Sci. Total Environ.* 664, 72–78.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344.

He, Q., Qiu, Y., Liu, H., Sun, X., Kang, L., Cao, L., Li, H., Ai, H., 2017. New insights into the impacts of suspended particulate matter on phytoplankton density in a tributary of the Three Gorges Reservoir, China. *Sci. Rep.* 7 (1), 1–11.

He, Q., Kang, L., Sun, X., Jia, R., Zhang, Y., Ma, J., Li, H., Ai, H., 2018. Spatiotemporal distribution and potential risk assessment of microcystins in the Yulin River, a tributary of the Three Gorges Reservoir, China. *J. Hazard. Mater.* 347, 184–195.

Heisler, J., Glibert, P., Burkholder, J., Anderson, D., Cochlan, W., Dennison, W., Gobler, C., Dortch, Q., Heil, C., Humphries, E., 2008. *Eutrophication and harmful algal blooms: a scientific consensus*. *Harmful Algae* 8 (1), 3–13.

Hu, H. J. and Wei, X. Y., 2006. The Freshwater Algae of China: Systematics, Taxonomy and Ecology. Science Press, Beijing, China (in Chinese).

Huisman, J., Jonker, R.R., Zonneveld, C., Weissing, F.J., 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology* 80 (1), 211–222.

Huisman, J., Arrayas, M., Ebert, U., Sommeijer, B., 2002. How do sinking phytoplankton species manage to persist? *Am. Nat.* 159 (3), 245–254.

Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Kardinaal, W.E.A., Verspagen, J.M.H., Sommeijer, B., 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology* 85 (11), 2960–2970.

Kang, L., He, Y., Dai, L., He, Q., Ai, H., Yang, G., Liu, M., Jiang, W., Li, H., 2019. Interactions between suspended particulate matter and algal cells contributed to the reconstruction of phytoplankton communities in turbulent waters. *Water Res.* 149, 251–262.

Karp-Boss, L., 1996. Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Mar. Biol. Ann. Rev.* 34, 71–107.

Ko, C.Y., Lai, C.C., Hsu, H.H., Shiah, F.K., 2017. Decadal phytoplankton dynamics in response to episodic climatic disturbances in a subtropical deep freshwater ecosystem. *Water Res.* 109, 102–113.

Leupold, M., Hindersin, S., Gust, G., Kerner, M., Hanelt, D., 2013. Influence of mixing and shear stress on *Chlorella vulgaris*, *Scenedesmus obliquus*, and *Chlamydomonas reinhardtii*. *J. Appl. Phycol.* 25 (2), 485–495.

Li, G., Wu, Y., Gao, K., 2009. Effects of Typhoon Kaemi on coastal phytoplankton assemblages in the South China Sea, with special reference to the effects of solar UV radiation. *J. Geophys. Res.* 114 (G4), 1–9.

Li, H., Pan, G., 2015. Simultaneous removal of harmful algal blooms and microcystins using microorganism- and chitosan-modified local soil. *Environmen. Sci. Technol.* 49 (10), 6249–6256.

Li, H., Ai, H., Kang, L., Sun, X., He, Q., 2016. Simultaneous Microcystis algicidal and microcystin degrading capability by a single *Acinetobacter* bacterial strain. *Environmen. Sci. Technol.* 50 (21), 11903–11911.

Li, J., Li, R., Li, J., 2017. Current research scenario for microcystins biodegradation – a review on fundamental knowledge, application prospects and challenges. *Sci. Total Environ.* 595, 615–632.

Li, M., Xiao, M., Zhang, P., Hamilton, D.P., 2018. Morphospecies-dependent disaggregation of colonies of the cyanobacterium *Microcystis* under high turbulent mixing. *Water Res.* 141, 340–348.

Lin, I., Liu, W.T., Wu, C.C., Wong, G.T.F., Hu, C., Chen, Z., Liang, W.D., Yang, Y., Liu, K.K., 2003. New evidence for enhanced ocean primary production triggered by tropical cyclone. *Geophys. Res. Lett.* 30 (13), 1–4.

Mackenzie, B.R., Leggett, W.C., 1993. Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparisons. *Mar. Ecol. Prog. Ser.* 94 (3), 207–216.

Merel, S., Walker, D., Chicana, R., Snyder, S., Baurès, E., Thomas, O., 2013. State of knowledge and concerns on cyanobacterial blooms and cyanotoxins. *Environ. Int.* 59, 303–327.

Michallet, H., Mory, M., 2004. Modelling of sediment suspensions in oscillating grid turbulence. *Fluid Dyn. Res.* 35 (2), 87–106.

Missagh, S., Hondzo, M., Sun, C., Guala, M., 2016. Influence of fluid motion on growth and vertical distribution of cyanobacterium *Microcystis aeruginosa*. *Aquat. Ecol.* 50 (4), 639–652.

Naselli-Flores, L., Barone, R., 2000. Phytoplankton dynamics and structure: a comparative analysis in natural and man-made water bodies of different trophic state. *Hydrobiologia* 438 (1–3), 65–74.

Neilan, B.A., Pearson, L.A., Muenchhoff, J., Moffitt, M.C., Dittmann, E., 2013. Environmental conditions that influence toxin biosynthesis in cyanobacteria. *Environ. Microbiol.* 15 (5), 1239–1253.

Ni, L., Li, D., Rong, S., Su, L., Zhou, W., Wang, P., Wang, C., Li, S., Acharya, K., 2017. Characterization of extracellular polymeric substance (EPS) fractions produced by *Microcystis aeruginosa* under the stress of linoleic acid sustained-release microspheres. *Environ. Sci. Pollut. Res.* 24 (26), 21091–21102.

Pan, G., Chai, F., Tang, D., Wang, D., 2017. Marine phytoplankton biomass responses to typhoon events in the South China Sea based on physical-biogeochemical model. *Ecol. Model.* 356, 38–47.

Qin, B., Yang, G., Ma, J., Wu, T., Li, W., Liu, L., Deng, J., Zhou, J., 2018. Spatiotemporal changes of cyanobacterial bloom in large shallow eutrophic Lake Taihu, China. *Front. Microbiol.* 9 (451–451).

Rao, K., Zhang, X., Yi, X.J., Li, Z.S., Wang, P., Huang, G.W., Guo, X.X., 2018. Interactive effects of environmental factors on phytoplankton communities and benthic nutrient interactions in a shallow lake and adjoining rivers in China. *Sci. Total Environ.* 619 (620), 1661–1672.

Symons, C.C., Arnott, S.E., Sweetman, J.N., 2012. Grazing rates of crustacean zooplankton communities on intact phytoplankton communities in Canadian Subarctic lakes and ponds. *Hydrobiologia* 694 (1), 131–141.

Thomas, W.H., Gibson, C.H., 1990. Effects of small-scale turbulence on microalgae. *J. Appl. Phycol.* 2 (1), 71–77.

Thomas, W.H., Vernet, M., Gibson, C.H., 1995. Effects of small-scale turbulence on photosynthesis, pigmentation, cell division, and cell size in the marine Dinoflagellate *Gomaulax polyedra* (Dinophyceae). *J. Phycol.* 31 (1), 50–59.

Tsuchiya, K., Kuwahara, V.S., Hamasaki, K., Tada, Y., Ichikawa, T., Yoshiki, T., Nakajima, R., Imai, A., Shimode, S., Toda, T., 2015. Typhoon-induced response of phytoplankton and bacteria in temperate coastal waters. *Estuar. Coast. Shelf S.* 167, 458–465.

Tsuchiya, K., Kuwahara, V.S., Yoshiki, T.M., Nakajima, R., Shimode, S., Kikuchi, T., Toda, T., 2017. Response of phytoplankton and enhanced biogeochemical activity to an episodic typhoon event in the coastal waters of Japan. *Estuar. Coast. Shelf S.* 194, 30–39.

Wang, P., Shen, H., Xie, P., 2012. Can hydrodynamics change phosphorus strategies of diatoms? – nutrient levels and diatom blooms in lotic and lentic ecosystems. *Microb. Ecol.* 63 (2), 369–382.

Wiedner, C., Visser, P.M., Fastner, J., Metcalf, J.S., Codd, G.A., Mur, L.R., 2003. Effects of light on the microcystin content of *Microcystis* strain PCC 7806. *Appl. Environ. Microbiol.* 69 (3), 1475.

Wilkinson, A., Hondzo, M., Guala, M., 2016. Effect of small-scale turbulence on the growth and metabolism of *Microcystis aeruginosa*. *Adv. Microbiol.* 6 (5), 351–367.

Xiao, M., Li, M., Reynolds, C.S., 2018. Colony formation in the cyanobacterium *Microcystis*. *Biol. Rev.* 93 (3), 1399–1420.

Xu, H., Jiang, H., Yu, G., Yang, L., 2014. Towards understanding the role of extracellular polymeric substances in cyanobacterial *Microcystis* aggregation and mucilaginous bloom formation. *Chemosphere* 117, 815–822.

Yu, Q., Chen, Y., Liu, Z., de Giesen, N., Zhu, D., 2015. The influence of a eutrophic lake to the river downstream: spatiotemporal algal composition changes and the driving factors. *Water* 7 (5), 2184.

Yu, Q., Liu, Z., Chen, Y., Zhu, D., Li, N., 2018. Modelling the impact of hydrodynamic turbulence on the competition between *Microcystis* and *Chlorella* for light. *Ecol. Model.* 370, 50–58.

Zhang, H., Chen, R., Feipeng, Li, Ling, C., 2015. Effect of flow rate on environmental variables and phytoplankton dynamics: results from field enclosures. *Chin. J. Oceanol. Limn.* 33 (2), 430–438.

Zhang, W., Zhu, X., Jin, X., Meng, X., Tang, W., Shan, B., 2017. Evidence for organic phosphorus activation and transformation at the sediment–water interface during plant debris decomposition. *Sci. Total Environ.* 583, 458–465.

Zhou, J., Qin, B., Han, X., 2016. Effects of the magnitude and persistence of turbulence on phytoplankton in Lake Taihu during a summer cyanobacterial bloom. *Aquat. Ecol.* 50 (2), 197–208.

Zhou, L., Tan, Y., Huang, L., Huang, J., Liu, H., Lian, X., 2011. Phytoplankton growth and microzooplankton grazing in the continental shelf area of northeastern South China Sea after Typhoon Fengshen. *Continent. Shelf Res.* 31 (16), 1663–1671.

Zhu, M., Paerl, H.W., Zhu, G., Wu, T., Li, W., Shi, K., Zhao, L., Zhang, Y., Qin, B., Caruso, A.M., 2014. The role of tropical cyclones in stimulating cyanobacterial (*Microcystis* spp.) blooms in hypertrophic Lake Taihu, China. *Harmful Algae* 39, 310–321.

Zhu, W., Zhou, X., Chen, H., Gao, L., Xiao, M., Li, M., 2016. High nutrient concentration and temperature alleviated formation of large colonies of *Microcystis*: evidence from field investigations and laboratory experiments. *Water Res.* 101, 167–175.